

The University of Chicago

COORDINATING MECHANISMS OF THE SPINAL CORD

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY
1931

By
OTIS CLARENCE INGEBRITSEN

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CHICAGO, ILLINOIS

Reprinted from
GENETIC PSYCHOLOGY MONOGRAPHS
Vol. XIII, No. 6, 1933

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\$7.00 per volume
Single numbers \$2.00

MONTHLY
Two volumes per year

June, 1933
Volume XIII, No. 6

GENETIC PSYCHOLOGY MONOGRAPHS

**Child Behavior, Animal Behavior,
and Comparative Psychology**

COORDINATING MECHANISMS OF THE SPINAL CORD*¹

From the Psychological Laboratories of the University of Chicago

By

OTIS CLARENCE INGEBRITSEN

*Accepted for publication by K. S. Lashley of the Editorial Board and received in the Editorial Office, December 28, 1931.

¹This study was supported by a grant to Dr. K. S. Lashley from the Otho S. A. Sprague Memorial Institute.

Worcester, Massachusetts

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Entered as second-class matter December 1, 1925, at the post-office at Worcester, Mass., under Act of March 3, 1879.

GENETIC PSYCHOLOGY
MONOGRAPHS

THE LATERAL AND ANTERIOR
AND POSTERIOR PSYCHOLOGY

CONTRIBUTION TO THE
PSYCHOLOGY OF THE

PSYCHOLOGY OF THE

THE LATERAL AND ANTERIOR

CONTENTS

I.	INTRODUCTION	487
II.	PURPOSE OF THE STUDY	493
III.	ANATOMY OF THE RAT'S CORD	495
IV.	TECHNIQUES	498
	Operation	498
	Histological Technique	499
	Reconstruction	499
	Tests and Methods of Studying Behavior	500
	Cortical Stimulation	502
	Controls	502
V.	PROTOCOLS	503
	Cases of Double Section in the Cervical Region	503
	Cases of Dorsal Section in the Cervical Region	523
	Case of Complete Transverse Section of the Cord	527
VI.	EXPERIMENTAL RESULTS	531
	Summary of Protocols in Cases of Double Section	531
	Summary of Protocols in Cases of Dorsal Section and Complete Transection	540
	Attempts at Conditioning	541
VII.	DISCUSSION	543
	The Mechanism of Conduction	544
	Character of Recovery	545
	Mechanisms of Recovery	548
	Modifiability in Separate Spinal Segments	551
	REFERENCES	552
	RÉSUMÉ EN FRANÇAIS	554
	REFERAT AUF DEUTSCH	555



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I

INTRODUCTION

It is the rule rather than the exception for discussions and descriptions of tracts of the spinal cord to treat of them as if they had exclusive function and very specific limitations. Previous experimental evidence has indicated less specificity of function in the tracts of the cord than might have been expected from its known anatomical structure. From an examination of the literature it is apparent that there is a great deal of contradictory evidence regarding the fineness of localization in or the accuracy of the restriction of function to the anatomical paths of the cord. Destruction or impairment of tracts in the cord, supposedly having exclusive sensory or motor functions, is frequently not followed by permanent incapacity. Instances of this can be found in clinical material where the spinal cord has been impaired through injury or disease, as well as in animals subjected to experimental lesions of the cord. Physiologists and psychologists interested in behavior studies on animals have gathered a mass of evidence which seems to point to much less specificity of function of the tracts of the cord than that ordinarily indicated.

Brown-Séquard (2, 3) held that the paths subserving cutaneous sensation ascend the spinal cord entirely contralateral to the initiating sense-organs, the decussation of the afferent channels occurring soon after their entrance into the cord. He claimed to have

established this fact in guinea pigs, dogs, cats, rabbits, and sheep, by hemisection of the spinal cord. He maintained that injuries confined largely to one side of the cord produced motor paralysis on the side of the lesion and sensory paralysis or impairment on the side opposite the lesion.

Many experimenters working on animals have contributed a mass of conflicting evidence, some of which tends to support the Brown-Séguard hypothesis, and some of which is directly opposed to it. Their results furnish considerable evidence as to restitution of sensory and motor functions of the cord with some suggestions as to how this restitution takes place.

Sherrington (19) says that it was known at the time of Hippocrates and the time of Galen that an effect of lateral hemisection of the cord is to impair the motor and sensory functions of the parts of the body innervated by the spinal nerves behind and on the same side as the section. According to Sherrington's account, it was Cooper working on the dog in 1803 who first reported recovery of motor functions.

A number of investigators have made observations on recovery or partial restitution of sensory functions. Weiss (22) reported that after hemisection in the hindmost thoracic region in the dog there was sensory defect in the opposite limb for all kinds of cutaneous sensation and for muscular sensation. This depression was said to be permanent for the opposite limb, and some sensory deficiency was apparent in the hind limb on the same side. He found that a second section on the other side and one segment farther headward abol-

ished permanently all sensation posterior to the lesion. Osawa (12) and Borgherini (1) [cited by Sherrington (19)] performed two successive hemisections on the dog in the thoracic region at intervals of seven segments. Restoration of sensitivity was reported to be long delayed and imperfect. Ferrier (4), after observation of a monkey for a period of 18 days after hemisection in the dorsal region, described the effect as absolute paralysis (motor) on the side of the lesion and absolute loss of sensation on the side opposite the lesion. Turner's (20) experiments with hemisection of the cord in monkeys gave evidence that the normal course of sensations was up the opposite side of the cord. His findings agreed with the Brown-Séquard hypothesis, but he did find that restitution of sensation took place on the side opposite the lesion. In one case he reported that from the 53rd day on it was impossible to say which had been the anaesthetic limb. He performed a second operation, a hemisection on the opposite side and three segments farther forward in the dorsal region on the 68th day after the original operation and found no return of sensation or movement on the other side up to the 113th day after the original operation. Mott (10), working with monkeys, claimed that with the return of movement the apparent loss of sensibility disappears. Schafer (17) reported sensation not lost on the side of the lesion but dulled temporarily. After a few days, sensation returned on the side of the lesion, while at no time was there any loss of sensation on the side opposite the lesion. He performed experiments on the cat and the monkey.

Most workers seem to be in agreement that restitution of motor function does occur in the limb or limbs on the side of the hemisection. Weiss (22) found restoration of motor function for standing, walking, and running, in the course of some weeks. Movements of the affected limb became almost perfect and were well associated with movements of the other limbs. Mott (10) and Turner (20) are agreed that, after two months, return of movements is almost complete in monkeys with hemisection of the cord. Mott indicated that bilaterally associated movements were first to return and that only some time later would the animal be able to perform unilateral movements on the side of the lesion. He found that the higher the lesion was above the limb the quicker the return of motor function. Schafer (17) maintained that all movements except purely voluntary ones are restored in the limb on the side of the lesion but he did not define voluntary movements. Turner found no return of motor function in the hind limbs of the monkey after double hemisection of the cord in which the lesions were separated by three segments, but Osawa (12) and Borgherini (1) found restoration of motility in the hind legs of the dog after similar lesions with a separation of six or seven segments.

Restoration or restitution of function seems to be rather common after other types of section in the spinal cord. Sherrington (18) reported almost complete division of the posterior columns of the cord in the lower thoracic region of the monkey which was followed, after ten days, by no definite abnormality of

movement or sensation. Schafer (17), working with the cat and the monkey, made section of the dorsal cerebellar tract on one or both sides, section of the ventral cerebellar tract on one or both sides, and section of both dorsal and ventral cerebellar tracts on one side. Lesions of these tracts either together or singly produced no obvious symptoms. Sensation and motion seemed unimpaired and the pupil was unaffected. No obvious symptoms were noticeable even when some of the pyramidal fibers were included. Rothmann (16) was able to demonstrate the formation of motor habits in the monkey in the absence of any possible influence from the pyramidal tracts even when the rubro-spinal tract on the side of the hand to be used had been divided. Lashley and Ball (7) gave clear evidence that the maze performance of the rat does not depend on the integrity of any specific tracts in the spinal cord of the rat.

The evidence seems to indicate a more or less complete recovery or restitution of motor functions in animals subjected to lesion of the spinal cord. In the cases where animals have been observed over some time following the operation this seems to be undisputed except in the case of Ferrier's observations on hemisections in monkeys and Turner's work on double hemisection in the monkey. All workers here cited, with the exception of Weiss and Ferrier, are agreed that there is return of sensory function on the side opposite the lesion. Here again it seems to be a matter of time after the operation before the sensory functions of the cord are partly or fully restored. In the cases

where two lesions have been made there seems to be a relation between the number of intact segments separating the sections and the return of function in the members affected.

II

PURPOSE OF THE STUDY

It was the plan of this study to obtain some evidence relative to the problems of spinal conduction and recovery from effects of lesions in the spinal cord. With respect to normal conduction it was hoped that some evidence might be obtained on the rôle of long tracts and of arcuate fibers in sensory and motor organization, on the degree of specificity of tracts, and as to how much of coordinated behavior is spinal and how much is controlled by higher centers.

With reference to the character of recovery, questions have been raised as to whether recoverable symptoms are evidence of diaschisis or of destruction of normally functional paths. There are also the questions, whether the recovery is spontaneous or the result of a process of re-education, and, if the latter, in what manner re-education occurs. Is it a matter of vicarious acquisition of functions by tracts not normally involved or by more efficient utilization of residual functions?

Evidence was sought as to the limits of recovery. Here we have the questions of rate of recovery with and without exercise, the limits of accuracy of control, and the limits of complexity of coordination that are possible.

Lastly, it was hoped that some information might be obtained as to the mechanisms of recovery. Here we have to deal with the questions of capacity of re-

covery in isolated segments of the cord, distance of separation in cases of double block, and various dynamic factors that may be influential in recovery.

III

ANATOMY OF THE RAT'S CORD

The conduction paths of the spinal cord of the rat have not been completely described, but Lashley and Ball (7) have summarized the previous descriptions of tracts in the rat cord and have been able to add further details from their work. Their cases involved the interruption of all the tracts in the cervical cord in one or another animal and these tracts were traced in so far as they were revealed by the Marchi technique. Figure 1, which is a composite from figures in Plates 1

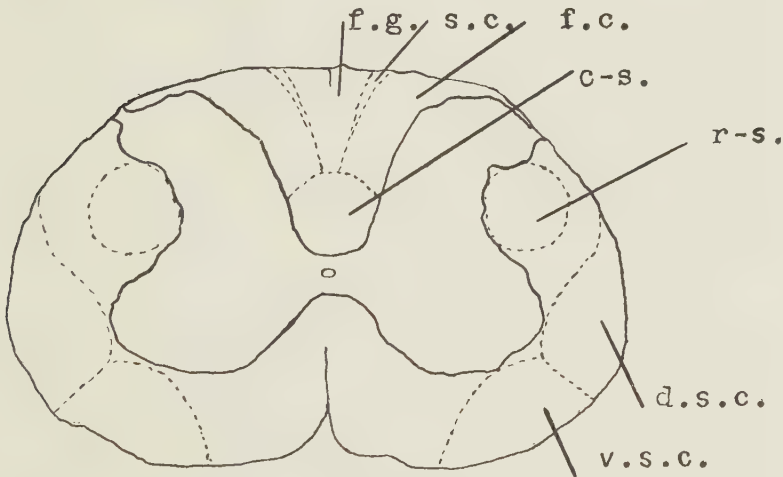


FIGURE 1

CROSS-SECTION OF THE CERVICAL CORD OF THE RAT, SHOWING
LOCATION OF THE PRINCIPAL TRACTS

f.g.—fasciculus gracilis
s.c.—Schultz's comma
f.c.—fasciculus cuneatus
c-s.—cerebro-spinal

r-s.—rubro-spinal
d.s.c.—dorsal spino-cerebellar
v.s.c.—ventral spino-cerebellar

and 2 of the Lashley and Ball study, shows the positions of tracts in the cervical cord of the rat so far as evidence at hand permits of their exact location.

Descending tracts figured are the cortico-spinal, the rubro-spinal, and Schultz's comma tract. The cortico-spinal tract occupies a median ventral position in the dorsal funiculus. The rubro-spinal tract is shown to be ventro-lateral to the dorsal horns. Schultz's comma tract is found between the fasciculus gracilis and the fasciculus cuneatus on each side.

Ascending tracts include the fasciculi gracilis and cuneatus of the dorsal funiculus, the fasciculus spino-cerebellaris dorsalis in the more dorsal part of the lateral funiculus, and the fasciculus spino-cerebellaris ventralis toward the ventral side of the lateral funiculus. No other ascending tracts are evident in enough detail in Marchi preparations to permit of description. It is probable that there are no long ascending or descending paths in the ventral funiculus of the rat.

Descending tracts other than those noted for the rat have been rather definitely located in the human cord. Villiger (21) describes tecto-spinal and vestibulo-spinal tracts, some of the fibers of which descend in the ventral funiculus and others in the lateral funiculus. He also describes a thalamo-spinal bundle in the lateral funiculus just medial to the ventral spino-cerebellar tract. Such tracts probably exist in the rat cord but staining methods have not been successful in their delineation.

Villiger describes no long ascending tracts in the

ventral funiculus of man. He indicates that there are in the lateral column spino-olivary, spino-thalamic, and spino-tectal connections. Lashley suggests, without conclusive evidence, the origin in the rat of spino-tectal fibers in the ventral funiculus. It seems probable that in the rat cord there are ascending fibers similar to those in man, but degeneration studies have not succeeded in demonstrating their exact location.

The arrangement of tracts in the cord of the rat is, with the exception of the cortico-spinal tract, similar to that obtaining in man, so far as is known. The evidence for variation in position of the cortico-spinal tract in different species has been summarized by Linowiecki (8). The work of Ranson (14, 15) and others has established the fact of complete decussation of the cortico-spinal fibers to occupy a median ventral position in the dorsal funiculus of the cord. There are no lateral or ventral pyramidal fibers in the rat cord. The rubro-spinal fibers probably cross in the midbrain as they do in man. The spino-thalamic tract is a crossed tract in the cord; others, so far as is known, ascend on the same side of the cord.

IV

TECHNIQUES

OPERATION

Operations were performed on adult rats in the cervical region, involving, in one animal or another, hemisection, double hemisection or section of the dorsal portion of the cord. In one case a complete transection of the cord was made at the level of the seventh thoracic root. Under ether anaesthesia and with aseptic precautions a slit about 15 millimeters long was made in the skin of the back of the neck and the muscle divided in the midline so as to expose the second cervical neural arch. After removal of this arch with bone forceps, an incision was made in the dura and then, by means of an iridectomy knife, one-half of the cord was severed from the midline to either right or left side. After injury to the cord the muscles and skin were united above the cord by interrupted sutures and the wound was dressed with cotton and parlodian. The cases put through two operations were subjected to similar procedure in the second one, except that the cord was exposed and sectioned farther caudad. The time that elapsed between first and second operations in the seven cases of double section reported in the results varied from 19 to 37 days.

Great difficulty was experienced in getting animals to survive a second operation and in many of the cases they did not survive the first operation. An attempt was made to have the two lesions as far forward in the

cord as possible in order to be in front of the innervation of the front limb on either side. Goering (5) has shown that the nerve supply of the brachial plexus of the rat begins with the fifth cervical root, and so it was usually attempted to make the more caudad lesion at that level or forward of it.

Porter's (13) work showed that in the dog and the rabbit the respiratory impulses pass down the lateral funiculi of the cord to reach the phrenic nuclei at the fourth cervical level. This suggests that the high mortality among cases subjected to double lesion may have been due to interference with or blockage of respiratory impulses. The work of Lashley and Ball (7) does not support this conclusion, since they succeeded in making complete section of both lateral columns at the second cervical level.

HISTOLOGICAL TECHNIQUE

The Marchi staining technique to show degeneration could not be used because of the long time interval between operation and necropsy, consequently a general fiber stain was used. Horizontal serial sections of each cord specimen were prepared and stained by Morgan's (9) iron-hematoxylin method for fiber.

RECONSTRUCTION

This included measurement of each section with identification of major tracts and plotting of the lesion on cross-sectional diagrams made from camera-lucida drawings of cross-sections in the cervical cord.

TESTS AND METHODS OF STUDYING BEHAVIOR

1. *Tests of sensitivity* were used at various times after operation. They included such things as pinching, pricking, and faradic stimulation of the skin, pulling hairs, attaching a clip to the skin of the flank or foot. It was difficult to make any adequate test of tactile sensitivity, but evidences of it were obtained at times when, after a series of faradic stimuli, the animal would squeal to touch alone or to stroking of the hair.

2. Observations were made on *motor control* in standing, walking, running, climbing, digging, etc.

3. *Head-limb coordinations* were noted where such evidence could be obtained and they were tested by using adhesive tape over the vibrissae on one or both sides to stimulate use of fore or hind limbs.

4. *Motor learning* was tested by the use of an elevated runway $1\frac{1}{2}$ inches wide and about 1 meter long, by the use of a simple T-maze (Figure 2), by the latch-box (Figure 3), and the digging-box.

The elevated runway gave an opportunity to observe the ability of the animal to orient itself and to main-



FIGURE 2
SIMPLE T-MAZE

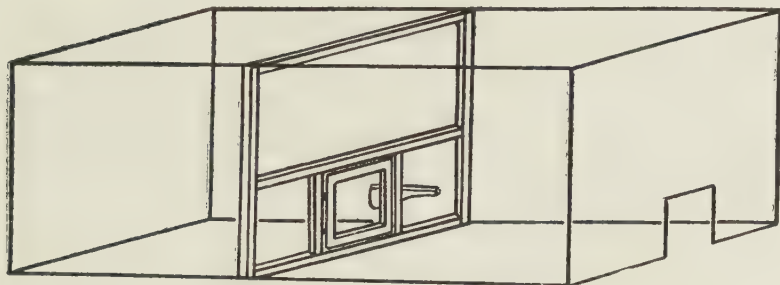


FIGURE 3
LATCH-BOX

tain its balance under conditions where the normal animal very readily does both. The simple maze afforded evidence of the ability of the animal to form motor habits requiring integration of a series of acts. The latch-box was used to obtain evidence of ability to manipulate devices with the hand and served therefore as a test of finer movements. A removable partition between starting compartment and food compartment in the latch-box allowed the substitution of latch-mechanisms in different positions when the animal had learned one. They were first tried on a problem requiring manipulation of a lever placed at the left side of the door and at a distance of about 3 inches from the floor. Next, a similar lever was used on the opposite side of the door. Finally, to test the animal's ability to get up on its hind legs and reach up for manipulation, the lever was placed about 8 inches above the floor.

On the latch-box the animals were given about five minutes to explore and to feed in the apparatus for

three days preceding the regular runs. They were given five trials per day until their time records showed no further improvement. With the maze they were given three days feeding in the food-box and then five trials daily until they reached a criterion of ten errorless runs on two days.

CORTICAL STIMULATION

The motor cortex was explored in most of the cases by means of bipolar stimulation. This was done to obtain evidence of limb movements; however, since limb movements are sometimes difficult or impossible to elicit in the normal animal, the results may not be very significant.

CONTROLS

A group of normal animals was used on the various pieces of apparatus for purposes of control.

V

PROTOCOLS

CASES OF DOUBLE SECTION IN THE CERVICAL REGION

Animals used for operation were all mature, one hundred days of age or more at the time of the first operation.

No. 1. Female Albino

Lesions. Figure 4A shows the maximum extent of the lesion on the right at the level of the second cervical root. This lesion interrupted all of the right side of the cord with the exception of part of the dorsal and ventral funiculi. Only a small part at the right side of the cortico-spinal tract has been injured. Tracts completely interrupted are the fasciculus cuneatus, the dorsal and ventral cerebellar tracts, and the rubro-spinal tract. The second lesion (Figure 4B), at the level of the fourth cervical root on the left side, has crossed the midline, and, slanting toward the left, has interrupted all of the left half of the cord with the exception of a small part of the lateral funiculus. At this level the tracts of the dorsal funiculus have been completely severed on both sides with the exception of a small portion of the right fasciculus cuneatus. All known long tracts on the left side of the cord have been severed except the ventral spino-cerebellar tract.

Sensitivity. Tests after the second operation gave no evidence of pain sensitivity up to the ninth day after the second operation. More than 30 days

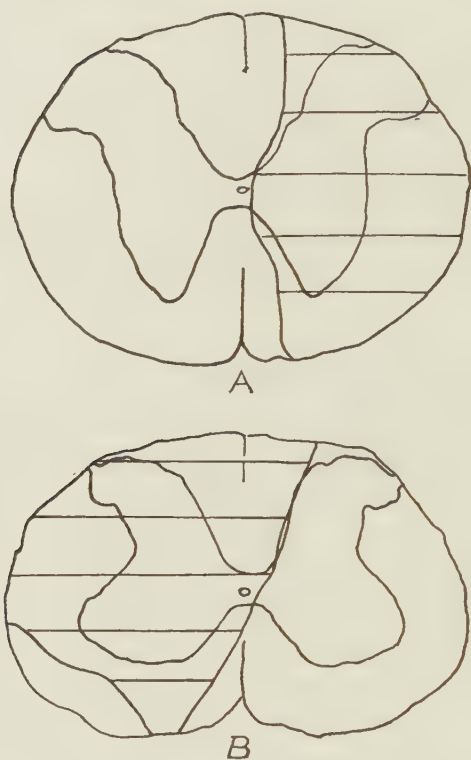


FIGURE 4

after the second operation the animal amputated a forefoot and seemed to suffer no pain from the wound. She had to be killed because of infection in the wound a few days later so that tests were not completed in her case.

Motor coordination. She was quite capable of standing, walking, running, and climbing within 20 days after the second operation. She was tried but once on the elevated path and she could not cling to it

at that time. This was on the eighth day after the second operation.

Head-limb coordinations. Two days after the second operation, when the left forepaw was brought up to the ear in what appeared to be a face-washing movement, the left hind foot moved synchronously with it. On the eighth day after the second operation she was able to use the left hand in face washing but the right was ineffective in this act.

Motor learning. She was tried only on the latch-box. On the fourth day her average time for the performance was 3 seconds which approximates the speed of the normal animal. She showed a ready transfer to the latch on the opposite side of the door.

For this animal, with no long tract intact except the ventral spino-cerebellar tract on the left side, the only impairment which remained very prominent was the evident analgesia and motor impairment of the right forepaw.

No. 2. Female Albino

Lesions. The lesion on the left at the second cervical level included the whole dorsal funiculus on both sides of the midline and interrupted all of the left side of the cord with the exception of the ventral funiculus (Figure 5A). All ascending tracts of the dorsal funiculus have been cut at this level as well as the whole descending cortico-spinal tract. The rubro-spinal tract, the dorsal and ventral spino-cerebellar tracts on the left have all been completely interrupted.

The lesion on the right at the fifth cervical root inter-

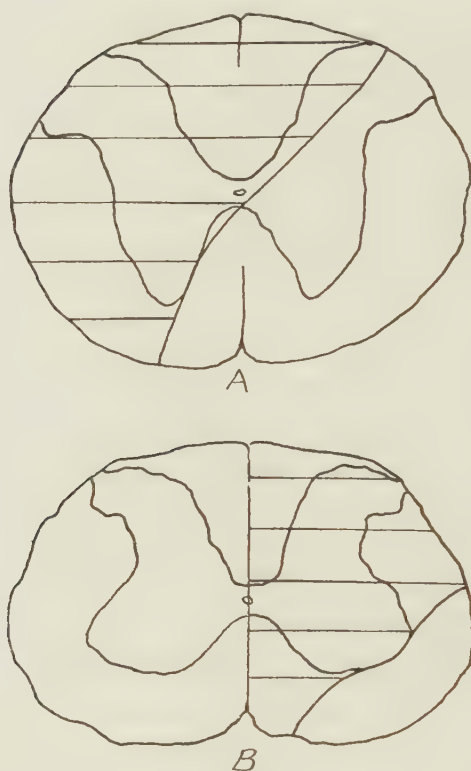


FIGURE 5

rupted all of the right side of the cord with the exception of the ventro-lateral portion of the lateral funiculus. Thus, on this side of the cord, all long tracts were cut except the ventral spino-cerebellar tract and a part of the dorsal cerebellar tract (Figure 5B).

Sensitivity. Cutaneous and pain sensitivity were apparent after the second operation. There were apparent defects in proprioceptive sensitivity, evidenced

by the animal's walk on the elevated pathway and by the fact that she frequently stepped on the dorsum of the right foot in walking on a smooth surface.

Motor control. Locomotion on flat surfaces became almost perfect after some time, although there was always much difficulty apparent in the walk on the elevated pathway. She was able to bring the left hand up to the latch in manipulating the latch-box, but very seldom made use of the hand in opening the mechanism. She used the forepaws in digging, never accompanying this by movements of the hind legs to scratch away accumulated shavings.

Head-limb coordinations. When the vibrissae were taped, she was able to remove the tape from the right side by the use of the right forepaw; only ineffectual movements with the left forepaw occurred in such instances. I once noted scratching of the nose and ear on the left side by the left hind foot. The right hind foot was freely used for scratching.

Learning. On the elevated pathway this animal was tried for one week, several trials a day, before she succeeded in walking the entire length of the path, a distance of one meter, without falling to the net below. Her progress was always slow and much difficulty was evident in balancing, for her chin was pressed down hard on the walk and the right forepaw was thrust over the right side of the pole with the fingers widely fanned out. She reached the criterion on the maze but trial and error records were considerably poorer than those of any normal animal. She learned the latch-box manipulation in any of the positions used in this prob-

lem, and reduced her time of performance to approximately that of a normal animal.

Cortical stimulation. No limb movements were obtained to stimulation of the left motor cortex. A very slight adduction of the left forepaw was obtained to strong stimulation of the right motor cortex.

In this case, with all known long tracts severed except the spino-cerebellar tracts on the right side of the cord, there was little evidence of impairment except for some of the finer movements of the left forepaw. There was clear evidence of conduction past the block in the cord. Complexity of integration seemed to approach that of the normal animal since she was able to learn although she took longer to reach the criteria of learning than did normal animals.

No. 3. Female Albino

Lesions. On the right side at the second cervical level the whole right half of the cord was severed with the exception of the most ventro-lateral portion of the right lateral funiculus (Figure 6A). The lesion on the left (Figure 6B) side at the level of the fourth cervical root included the right fasciculus gracilis and cut all the left side of the cord except the ventral funiculus. Long tracts completely severed in this cord were the fasciculi gracilis and cuneatus, the cortico-spinal, the dorsal cerebellar on the right, and both rubro-spinal tracts. Tracts remaining were the left ventral spino-cerebellar tract and parts of the left dorsal spino-cerebellar tract, together with a portion only of the right ventral spino-cerebellar tract.

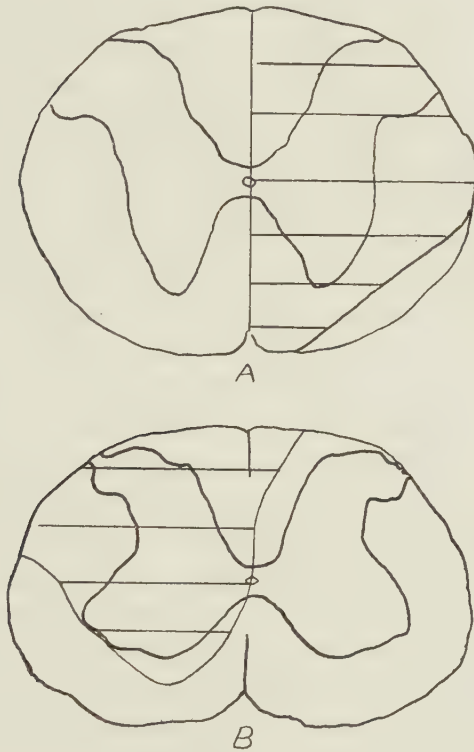


FIGURE 6

Sensitivity. Tests at various times did not show any marked degree of impairment in pain sensitivity. She responded to pinching, pricking the skin, electrical stimulation, and pulling hairs, much the same as does a normal animal. She squealed to all these stimuli and reacted to the position of the stimulus. There was doubtful evidence of tactile sensitivity since there was not much squealing to contact on any part of the body

after electrical stimulation. The most evident permanent impairment was in proprioceptive sensitivity.

Motor control. After the first operation the animal moved for some days chiefly by twisting to the left side. She fell to the left side frequently and had difficulty in righting herself. There was a slow improvement in locomotion up to the time of the second operation. Two days after the second operation she again showed the twist to the left side in locomotion, and the right limbs were less perfectly controlled than the left. She sidled to the left with the body highly arched, frequently falling to the left side. Her progress along the elevated pathway was slow and, as she went, the right forepaw was over the edge, making contact with the side of the pole at each step that she took. Difficulties that did not appear in her walk on a flat surface showed very plainly on the elevated pathway. The limbs were moved in the same order as those of the normal animal but the control of the limbs was far from normal at any time. Her head was kept down close to the right side of the pole as she walked on it. In the latch-box she used the left hand exclusively, no matter in what position the lever was placed. The left forepaw was much more effectively used in digging than was the right. Both hands were used, but the right moved stiffly, while she often used her mouth to help remove shavings from the doorway.

Head-limb coordinations. Face cleaning with the left hand occurred four days after the second operation. She was able to remove adhesive tape from the left vibrissae by the use of the left forepaw; the right

made only ineffectual movements when the right vibrissae were taped. In the latter case the right hand was thrust forward but did not reach the face. Although there was scratching of the neck region by the left hind foot, I never observed scratching in the head region by the right hind foot.

Motor learning. It took her some days to learn to walk the elevated pathway. The greatest difficulty was in control of the hind legs, which were allowed to hang over the edges of the walk when the animal was placed on the runway, and frequently slipped over the sides as she attempted to move forward. Although in her first attempts she often fell to the net below, she finally mastered the task and walked the whole distance without falling. On the latch-box she was slow to react, never reducing her average time to equal that of a normal animal. She reached the criterion of learning in the maze, with trial and error records much poorer than those of the poorest normal record.

Cortical stimulation. The only movement in response to stimulation of the motor cortex was adduction of the left forepaw.

This case, with all long tracts interrupted except the ventral spino-cerebellar on the left side, showed little sensory impairment except for proprioception. Stimuli in the head region passed the block in the cord and aroused movements of all limbs except the right hind limb. I had no evidence of the use of the latter member in response to head stimulations. She was generally slower than a normal animal but she succeeded in learning all the problems presented to her.

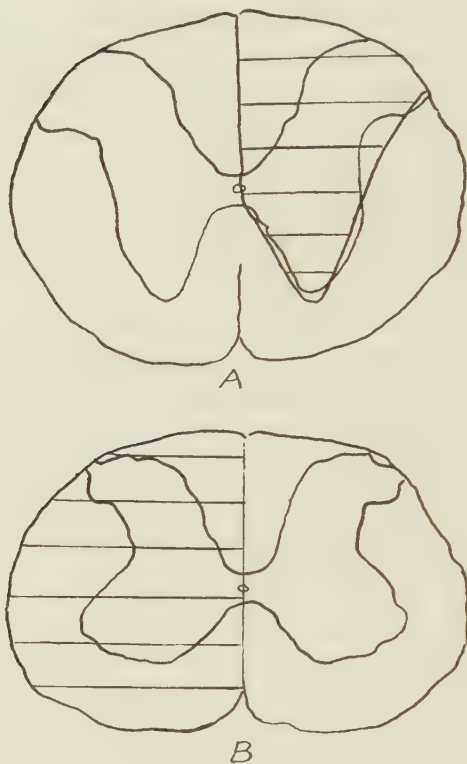


FIGURE 7

No. 4. Hooded Male

Lesions. The lesion at the right at the first cervical level was not a complete hemisection. It interrupted only the dorsal funiculus on the right side and all of the gray matter (Figure 7A). The lesion on the left side four segments farther caudad (Figure 7B) was a complete hemisection. In this animal the only long tracts left intact were those of the right lateral

funiculus: the right rubro-spinal, the dorsal and ventral spino-cerebellar tracts.

Sensitivity. When tested at different times by means of pulling hairs, pinching the skin with forceps or clips, or with electrical stimulation of the skin, he seemed equally sensitive on either side of the body. In some instances it did seem that he was more sensitive on the left side than on the right side, judging by the strength of stimuli that was required to elicit squealing, but this behavior was too variable to warrant any definite conclusion. Cleaning activity on both sides of the body was frequently noted in this animal even though there was a complete interruption of the left side of the cord.

Motor control. After the first operation there was much turning to the left side up to the end of the second week when the walk had very much improved, although it was slow and the back was highly arched. After the second operation there was little locomotion for some days and the animal crawled about chiefly by the use of the right forepaw. The full use of the left forepaw in walking never was recovered although the animal was kept under observation for a year after the second operation. In the latch-box he adhered strictly to the use of the right hand, no matter in what position the lever was placed. When feeding on pellets, he always grasped them with the right hand, using the left fist to brace against the food. In the digging tests he used both hands, although the left one was not very effective in the act. He, too, used the mouth to assist in removing shavings from the doorway.

Head-limb coordinations. Effective face washing was done with the right forepaw and it was used for the removal of adhesive tape from the right vibrissae. The left forepaw was brought up in the face-washing gesture, but it never made contact with any parts above the mouth, so that he was not successful in removing adhesive tape from the left vibrissae with this hand. The hind leg on the right was quite freely used for scratching-reactions to the head region; the hind leg on the left was rarely used for such reactions although I noted on several occasions scratching of the left ear by the left hind foot. This movement was noted once when adhesive tape had been placed over the left vibrissae.

Motor learning. He could not walk the elevated pathway when first tried on it, six months after the second operation. It was only after many falls from it that he learned to keep all feet placed on top, and then the left forepaw was always closed in a fist as he progressed. He reached the criterion on the maze but his trial and error records were poorer than those of any normal animal. With practice on the latch-box he learned to operate the mechanism in about the same time as a normal animal and had no trouble in transferring from one lever position to another.

Cortical stimulation. Stimulation of the frontal areas of the cortex produced movements of the forelegs only. The left foreleg showed adduction in response to stimulation of the right cortex and the right foreleg adduction to stimulation of the left cortex.

This animal, with complete block of the cord on the

left side, and only lateral and ventral tracts on the right side intact, showed no particular sensory impairment, and motor impairment of the left forepaw for finer movements only. There was clear evidence of conduction from the head region past the block in the cord. He was able to adapt to the elevated pathway and to the digging-box, and demonstrated no marked disability in acquisition of latch-box and maze integrations.

No. 5. Female Albino

Lesions. The lesions in this case were practically the same as for those of the animal just reported, except that they were reversed in position and two segments closer together. The lesion on the left, at the second cervical level, extended down the midline beyond the level of the ventral median fissure, including a part of the left median ventral funiculus. It severed the left gracilis and cuneatus and the left half of the cortico-spinal tract and took in all of the gray matter on the left side (Figure 8A). The lesion at the right was a practically complete hemisection at the level of the fourth cervical root (Figure B). The only intact long tracts in this cord were those of the left lateral funiculus, namely, the rubro-spinal and the dorsal and ventral spino-cerebellar tracts.

Sensitivity. There was no evident difference in this respect between this animal and No. 4 previously reported.

Motor control. After the first operation the left forepaw seemed to be much more seriously affected than the left hind leg. She frequently stepped on the

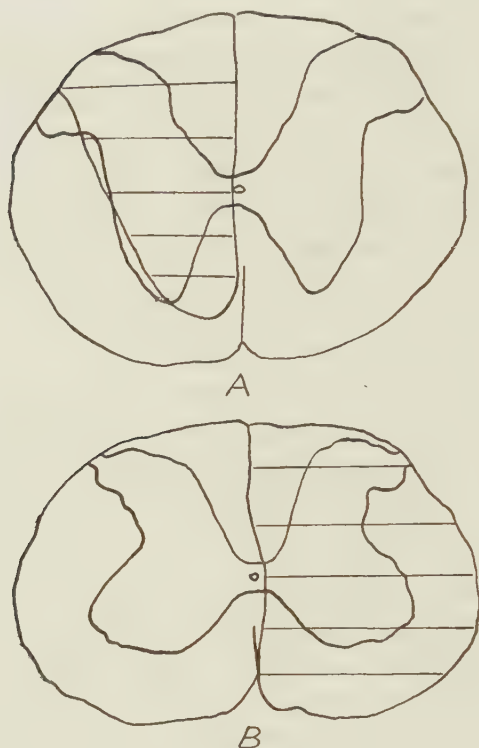


FIGURE 8

dorsum of the left forepaw. For a time after the second operation she lay on her side with all feet sprawled in the air, and, on beginning to walk, she twisted to the left side, frequently falling to that side. At this time the toes of the right forepaw were flexed and both legs on that side were thrust far out to the side as she walked. About two weeks later she had recovered to the point of having a sort of duck-waddle gait, staggering somewhat but not falling frequently. She showed

lack of motor control, which might have been due to proprioceptive disturbances, when first tried on the elevated walk. The latch-box demonstrated quite free use of her left hand, which was the hand most used in the tests with the digging-box.

Head-limb coordinations. She evidenced quite complete recovery of all members except the right forepaw. This was never used for face cleaning after the second operation, but was thrust forward in the face-cleaning gesture. When the vibrissae were taped the hind foot on the right scratched the face and ear region.

Motor learning. Tried on the elevated pathway about five months after the second operation, she did not show much disturbance of locomotion. All feet were kept upon the walk except the right forepaw which slid along the right edge of the path as she progressed. Her nose was always kept near the right edge of the pole, a posture which was an evident factor in balancing. She was very slow in the maze and did not reach the criterion in any case. She was given 100 trials on one side, more than the number required by any other operated case to reach the criterion, and 151 trials on the other side, which was half as many again as any other operated case required to reach the criterion. This was the more surprising in that, after the failure on this problem, she showed very clear evidence of retention of an 8-cul-de-sac maze which had been learned five months earlier after the first operation. Her record on the retention problem indicated a saving of 62% over the original trial record and

about 85% of the original error record. She was slow on the latch-box, although she did learn to operate the mechanism in all different positions. Her time was considerably longer than that of any other operated case.

Why this animal, with not much more severe impairment of the cord than that described for No. 4, had so much difficulty with the learning problems is a question that is not at all clear. It might be attributed to the fact that the lesions in this case were separated by only one segment of cord and therefore would give less opportunity for restoration by means of arcuate channels. This animal seemed always to be in poor physical condition, no matter how well she was fed and cared for. There was evidence of conduction past the block on the right side of the cord. Her greatest difficulty seemed to be in the acquisition of new adaptations such as those which the maze problem and the latch-box offered.

No. 6. Female Albino (used as a normal control on the maze and latch-box previous to operation)

Lesions. The lesion on the left side at the second cervical level was a complete hemisection (Figure 9A). The lesion on the right side at the level of the fifth cervical root (Figure 9B) interrupted the fasciculus gracilis on both sides of the midline, the right fasciculus cuneatus, the right half of the cortico-spinal tract, all of the gray matter on the right, and the dorsal portion of the right lateral funiculus. The only long tracts remaining intact in this cord were the dorsal and

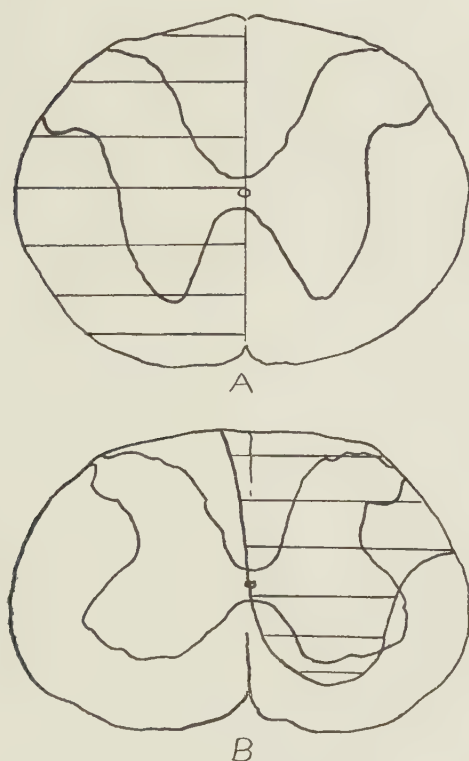


FIGURE 9

ventral spino-cerebellar tracts on the right side. The ventral funiculus on the right had been left almost intact.

Sensitivity. Three months after the second operation she reacted to all types of stimulation on the skin as a normal animal does. Following a series of rather strong faradic stimuli, she would squeal to touching with a pencil point, stroking the hair gently, or to mere contact with the hand.

Motor coordination. Since most other animals had not been tried on the elevated pathway until some time after the second operation, I was most interested to see whether they could adapt to this situation soon after operation. Eight days after her second operation this animal was able to go the distance of one meter without falling to the net. With the hind legs astride the pole, she clung like a sailor on a rope, using the right hind foot, which sometimes made contact with the side of the pole, to propel her body. Her behavior gradually improved for a month or more following this time until she was able to keep her feet on the pole most of the time. The right forepaw was readily used for digging while the left was not very effectually used. In the latch-box the left hand was sometimes brought up to touch the under side of the lever although she always manipulated the lever with the right hand.

Head-limb coordinations. I noted scratching of the right ear with the right hind foot. No such activity on the part of the left hind foot was ever noted. In face washing, although the left hand was cupped and moved coordinately with the right, it never made contact with the mouth. Adhesive tape over the left vibrissae was never removed. The right forepaw was readily used in removing adhesive tape from the right vibrissae.

Motor learning. Retention tests on the latch-box with the lever in the low position in which it had been learned before the operation showed practically no loss in average time of performance. Tried later on the latch-box with the lever in the high position, she

readily learned to manipulate it and always used the right hand in doing so. Her behavior on the elevated pathway has already been described.

This animal, with no long tracts intact except the spino-cerebellar tracts of the right side, demonstrated a rather complete recovery of gross motor functions such as those involved in locomotion, climbing, and maintenance of equilibrium on floor or elevated walk. There was no sign of permanent impairment in cutaneous sensitivity. There were some signs of persistent proprioceptive deficiency. Manipulation of the latch-box mechanisms and the ability to dig through an obstruction were not impaired by the destruction of a large cross-sectional area of the cord. There was evidence of retention of the latch-box habit which had been learned before operation.

No. 7. Female Albino (used as a normal control before operation)

Lesions. The lesion on the left side at the second cervical level had crossed the midline interrupting the fasciculus gracilis on the right side. All of the left half of the cord had been severed except a very small portion of the most medial left fasciculus gracilis and cortico-spinal tracts together with the most medial portion of the median ventral funiculus (Figure 10A). The lesion at the right side in the region of the fifth cervical root (Figure 10B) interrupted the whole right half of the cord with the exception of the fibers of the ventro-lateral funiculus. It is possible that the

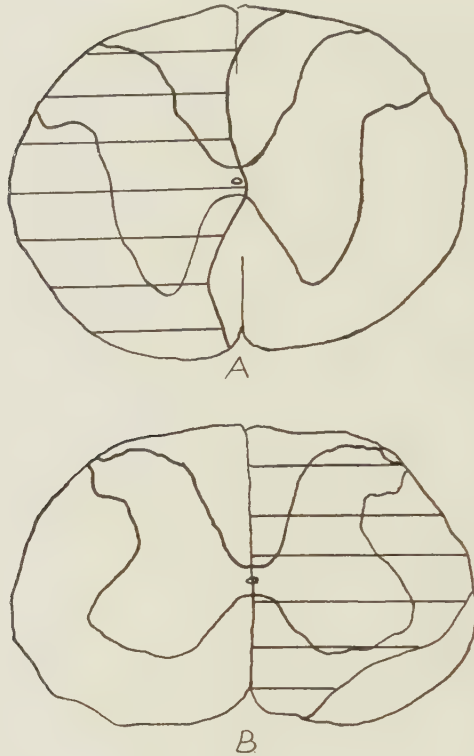


FIGURE 10

only functional long fiber tract in this cord is the right ventral spino-cerebellar tract.

Data. In treatment and observations this animal was an exact parallel of No. 6 described above. So far as her behavior is concerned, there is nothing to add to the account given above except in one instance. I did note use of the left hind leg for scratching in the head region in this animal. The left forepaw showed the same sort of impairment as that already described

for No. 6, that is, it was ineffective in face washing and could not be used to remove adhesive tape from the left vibrissae.

Cortical stimulation. Stimulation of the left cortex produced adduction of the right forepaw and dorsiflexion at the wrist. Stimulation of the right cortex was followed by adduction of the left forepaw and dorsiflexion at the wrist, and, at one time, the foot was very definitely thrust forward. No movements of the hind legs were elicited.

CASES OF DORSAL SECTION IN THE CERVICAL REGION

No. 8. Hooded Female

Lesion. The lesion, which was at the level of the second cervical root, interrupted most of the dorsal half of the cord. All tracts of the dorsal funiculus were cut, together with both dorsal horns of gray matter. There was partial interruption of both rubro-spinal tracts (Figure 11).

Sensitivity. There was evidence of proprioceptive deficiency at first, but this was not permanent.

Motor control. On the first day after the operation the hind legs were spread out from the body at an angle of about 90° and moved in a wide arc as the body was propelled on the table. The hind part of the body was lifted a little. The toes of the forepaws were clasped into fists and the animal sometimes stepped on the dorsum of a forepaw. The hind legs sprawled over the edges of the elevated pathway and were not drawn up. She showed gradual improvement in her walk on a table and on the elevated pathway during the

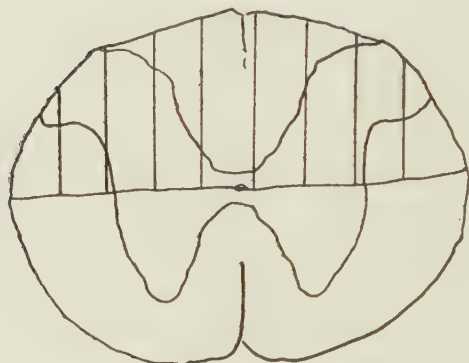


FIGURE 11

following days. For some days the hind feet slipped back when she was walking on a smooth surface and one or the other was dragged now and then. The forepaws were dragged as she swung her body from side to side during the first few days. She sometimes stepped on the dorsum of the forepaws but most frequently the toes were spread as the foot was placed. She gradually obtained better control of all feet and they were brought in closer to the body line in walking. She used either hand or both in manipulating the lever in the high position in the latch-box. She used both hands in digging through shavings to food and seemed to use them equally well.

Head-limb coordinations. She used her hands in clumsy fashion to wash her face shortly after the operation. Within ten days after the operation she readily removed adhesive tape from the vibrissae on either side by the use of the hand on the same side. I frequently observed scratching of head and nose by the hind leg on either side.

Motor learning. On the elevated pathway four days after operation, she managed to move a short distance along it but the movements looked more like swimming than like walking. All feet were astride the pole and their movement made sufficient contact with the pole to cause some progression. Her first trip from end to end of the pole was made in this fashion a few days later. Fifteen days after operation she walked the whole length of the pole without showing much disability. There was some tendency to allow a foot to hang over the side of the pole, particularly when at rest, even up to the time of autopsy. She learned to manipulate the latch-box without difficulty. She was not tried on the maze.

Cortical stimulation. Clear movements of the right forepaw and the right hind foot were obtained in response to stimulation of the left motor cortex. Movements of the left hind limb followed stimulation of the right motor cortex but no clear movements of the left forepaw were obtained.

This animal, with the dorsal funiculus completely severed and some injury to the rubro-spinal tracts of both sides, showed little evidence of permanent impairment so far as the tests used permit of a conclusion. At the end of an observation period of one and one-half months her behavior was in every respect very much like that of a normal animal.

No. 9. Hooded Female

Lesion. The lesion at the second cervical level interrupted both dorsal horns of gray matter, all of

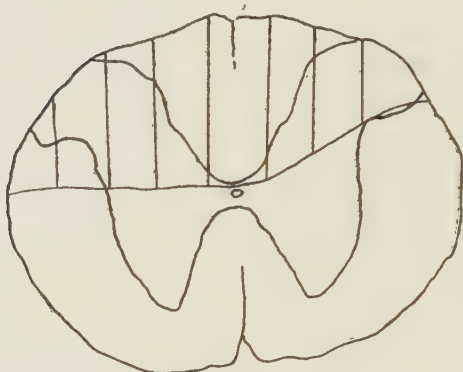


FIGURE 12

the dorsal funiculus, and a portion of the left lateral funiculus. Tracts cut were the fasciculi gracilis and cuneatus of both sides, the cortico-spinal tract, and a part of the rubro-spinal tract on the left side (Figure 12).

Sensitivity. No apparent differences could be discovered between this animal and No. 8 in this respect.

Motor control. In general, motor control was much the same as that reported for No. 8, except that it was restored to a semblance of normal behavior at an earlier date than for the above animal. Her hind legs were not sprawled out from the body so widely as were those of No. 8. On the fourth day after the operation her walk on a table was very much like that of a normal animal. Within 20 days following the operation the only tests that seemed to distinguish her from a normal animal were those on the elevated pathway and on climbing or clinging to a vertical pole.

Control of the hind legs on the elevated pathway seemed to be poor for some time. Otherwise her behavior seemed to be that of a normal animal.

Head-limb coordinations. From the fifth day after the operation face washing was normal and other reactions to stimuli in the head region were normal.

Motor learning. She readily learned to walk the elevated pathway, going the whole distance five days after operation. Control of the hind limbs returned to the point where she was able to walk the path about as well as a normal. She used both front and hind feet in digging through the shavings to food. The latch-box gave her no difficulty since she quickly learned to operate the lever in any position used. Preference for the right hand was indicated.

Cortical stimulation. Good clear movements of the forelegs were obtained in response to stimulation of the motor areas, the left foreleg showing adduction to stimulation of the right cortex and the right foreleg adduction in response to stimulation of the left cortex.

This case, with complete section of the long paths of the dorsal funiculus and injury to the left rubro-spinal tract, showed a marked recovery from injury in a very short time.

CASE OF COMPLETE TRANSVERSE SECTION OF THE CORD

No. 10. Female Albino

Lesions. Histological examination showed complete transection of the cord at the level of the seventh thoracic.

Sensitivity. There was no evidence at any time

after the operation that this animal was sensitive to stimulation on the rear part of the body or the hind legs. Faradic stimulation and break shocks were used in varying strength, pinching, pricking the skin, and pulling hairs. In response to none of these stimuli was there any squealing. When suspended by means of a belt passed about the body, and subjected to stimulation which would cause squealing in a normal animal or in an animal with two sections at different levels of the cord, she would go right on with face washing and give no evidence of emotional disturbance. There was never any cleaning of the rear parts of the body.

Reflexes. Reflexes of the hind limbs were depressed for a short time only after the operation, and then fully recovered. A half hour after the operation there were good reflex movements of the hind limbs. If the animal was suspended, stimulation of one leg would cause flexion in that member and extension in the opposite one. Pinching the tail caused a sort of mass reflex of the whole rear portion of the body. Scratch reflexes of the hind leg would follow stimulation of the corresponding flank or side of the abdomen at about the nipple line. In the early period of observations defecation and urination did not occur without extra stimulation. When the bladder became very full it was automatically emptied. It could be stimulated to empty its contents by stroking the abdomen gently or by tapping over the region of the bladder. Defecation occurred during the early days after operation when the animal was suspended for stimulation of any kind, and while such stimuli were being ap-

plied. This animal was kept for a little more than six months after the operation, during which time intermittent observations were made on her. Elimination of urine and feces became automatic some time after the operation. Mineral oil was used from time to time in order to prevent stasis.

General behavior and recovery data. The animal moved about very readily within a short time after the operation, using the front legs to support the fore part of the body and to propel the body. All activities of the fore part of the body were apparently normal. In locomotion, movements of the hind legs occurred only when some rough surface over which the body passed offered stimulation directly to the abdomen or to the legs themselves. Kicking movements of the hind legs sometimes occurred if the bladder was distended. When the experimenter took the animal and pulled her along on a smooth surface there were no stepping movements of the hind legs. When hanging by the forepaws to a pole she did not move the hind legs in any endeavor to climb up onto the pole. She often climbed up the side of the cage using the forepaws only. There was no evidence of any sensory or motor recovery of the hind limbs so far as "voluntary" control of movements of the rear part of the body was concerned. No evidence was obtained which would indicate passage of an impulse around the block in the cord. This animal was used over a long period of time in an attempt to establish conditioned reflex of the left hind leg. She gave no evidence of conditioning to the

originally indifferent stimulus which was a light contact on the leg.

Cortical stimulation. Clear movements of each of the forepaws were obtained but no movements of the hind legs.

VI

EXPERIMENTAL RESULTS

SUMMARY OF PROTOCOLS IN CASES OF DOUBLE SECTION

Long fiber tracts or parts of such tracts that remained intact are indicated for each animal. Any portion of the ventral funiculi that remained is also described. No. 1 had intact the left ventral and part of the left dorsal spino-cerebellar tract with the medium parts only of the ventral funiculus. In No. 2 the spino-cerebellar tracts on the right, and the left ventral funiculus, were intact. Marginal portions of the right spino-cerebellar tracts, complete left spino-cerebellar tracts, and a small part of the left ventral funiculus were uninjured in No. 3. No. 4 had intact the whole right ventral and lateral funiculi which meant that there was no injury to the right cerebellar tracts or the right rubro-spinal tract. Tracts remaining uninjured in No. 5 were the left rubro-spinal and the left spino-cerebellar tracts. A part of the left ventral funiculus also remained in this animal. No. 6 possessed only the right ventral funiculus and the right spino-cerebellar tracts. Portions not severed in the cord of No. 7 were the right spino-cerebellar tracts and a small median part of the left ventral funiculus.

In no case were there any demonstrated long ascending tracts intact except the spino-cerebellar, and they were confined to one side only with the exception of one case, No. 3, in which the left cerebellar tracts and a small portion of the right cerebellar tracts remained.

Since there are in man spino-olivary, spino-tectal, and spino-thalamic tracts which ascend in the lateral funiculus, it is probable that such tracts or portions of them were intact on one side in six of the seven cases of double cervical section.

Positions of such descending tracts as the vestibulo-spinal, tecto-spinal, and thalamo-spinal, which have been described in man, are not known for the rat, but it is probable that they occupy portions of the lateral and ventral funiculi. Assuming that such tracts exist in the rat and that they are situated as in the cord of man, it is probable that they were functional in some of our cases with double section in the cervical region. The cortico-spinal and Schultz's comma tracts were completely severed in all cases. The rubro-spinal tract was left intact on one side only in two cases, namely, Nos. 4 and 5.

Behavior and Recovery Data

Sensory disturbances. No evidence was obtained for permanent sensory disturbances apart from those which indicated proprioceptive defect except in the case of No. 1 which was apparently analgesic for the period of observation.

The most certain evidence for tactile sensitivity obtained in this study came from cases where electrical stimuli had been applied to various parts of the skin for some time. Following a series of electrical stimuli, squealing could be elicited by touching the animal on either side, stroking the hair, or even blowing on the hairs at some point. Animals showing this type of

response for both sides of the body were Nos. 5 and 6 of the protocols, as well as No. 4 which was used in conditioning experiments. No. 4 had a complete left hemisection; No. 5 had practically complete hemisection of the right side of the cord; and No. 6, a complete hemisection of the left side of the cord. This would seem to indicate that tactile impulses from both sides of the body may pass headward through the intact portions of one side of the cord.

Motor control. Coordinations of limbs for standing, walking, running, and climbing showed a gradual return in all the cases. There was some evidence that Nos. 4 and 5, with rubro-spinal tracts of one side intact in each case, recovered control more readily than other cases where such tracts had been completely severed. Hind limbs were less impaired for locomotion and recovered more quickly than forelimbs. The greatest impairment in the use of the forelimb was always on the side of the most complete lesion. Gross movements were recovered for the forelimb on the side of the most complete lesion in all cases, though the animals were never successful in using this forelimb for movements requiring finer adaptation, such as manipulation of a lever, grasping pieces of food, removal of adhesive tape from the vibrissae of the same side, or for effective face washing.

Comparison of No. 1 with No. 3 furnishes interesting evidence on recovery of finer manipulations of the hand. No. 1 suffered a greater lesion of the cord on the left side than the maximum lesion of No. 3, which was on the right side. No. 3 did not recover the use

of the right hand for finer movements but was able to use the left hand for face washing and manipulation of the latch-box mechanism. No. 1 had a complete lesion of all long tracts on the right side and it was noted that the left hand, in spite of severe injury on that side, recovered sufficiently for face-washing movements. Lack of recovery of the right hand in No. 3 may have been related to the fact that she could more freely use the left hand because of lesser injury on that side, while No. 1, forced to use the left hand in spite of severe injury on that side, showed considerable recovery of the member. This suggests that the degree of recovery is, within limits, less dependent upon the extent of injury than upon compulsory use of the limb.

Locomotion of a sort occurred in all cases within a few days after the second operation and, so far as observations go, the pattern of locomotion seemed to be that of the normal animal. No animal of the seven cases was ever observed to stand on the hind feet in the spontaneous fashion frequently exhibited by the normal animal. That they were able to do this was evidenced by their ability to stand on the hind legs in order to operate the latch-mechanism in the high position.

Head-limb coordinations. Animals with double section carried out body-cleaning operations similar to those of normal animals. They were able to react to the locus of a stimulus applied to the body caudad to the lesions. In all cases the forelimb on the side of the most severe or complete lesion was most impaired, although in cases of complete hemisection the fore-

limb on the same side could be thrust forward in an ineffective face-cleaning gesture if adhesive tape were placed over the vibrissae on that side. No. 4, with a clean left hemisection, was observed to use either the left or the right hind foot in scratching the ear or head. No. 5, with complete right hemisection of the cord, used the right hind foot for scratching the face and ear when adhesive tape had been applied to the vibrissae on the right side. She had quite free use of the left hind foot.

Motor learning. Records of normal animals in learning the simple T-maze are shown in Table 1. The

TABLE 1
INDIVIDUAL RECORDS OF LEARNING ON SIMPLE T-MAZE
NORMAL ANIMALS

Animals trained to go to food at the right side and then to go to food at the left side of the maze.

Rat No.	Maze records			
	Food Errors	at right Trials	Food Errors	at left Trials
11	2	6	8	31
12	7	41	9	16
13	6	16	12	26
15	12	21	10	16
16	7	11	9	16
17	8	31	10	26
18	6	21	9	16
19	8	16	9	16
20	5	11	7	16
21	9	21	8	16
22	9	26	15	26
23	8	16	11	31
24	7	26	13	26
25	6	16	7	26
26	9	21	9	31
27	9	41	12	31
28	7	21	9	31
Mean	7.4	21.3	9.8	23.4

TABLE 2

LEARNING RECORDS OF OPERATED ANIMALS ON SIMPLE T-MAZE
Animals trained to go to food at the right side and then to go to food
at the left side.

Rat No.	Maze records			
	Food at right Errors	Trials	Food at left Errors	Trials
2	16	66	18	41
3	41	66	21	91
4	18	56	15	36
5	43	101	37	151
Normal mean	7.4	21.3	9.8	23.4

animals were trained to go to food at the right side first, and, upon reaching the criterion, they were started running to the left side of the same apparatus. Table 2 shows the records of four animals with double section in the cervical cord, for the same maze problems. The average normal record is inserted in this table for purposes of comparison with the records of operated animals. In learning to go to food at the right, the operated animals made from two to six times as many errors as the average normal animal, and in learning to go to food at the left side, they again made from two to four times the number of errors made by the average normal animal. Of the operated cases run on the maze problems, one, No. 5, failed to reach the criterion of learning in either case in the number of trials given. She was given 101 runs to the right side and 151 runs to the left side without showing any tendency to cut down her record of about one error per day.

The learning progress on the latch-box is shown for

sec.

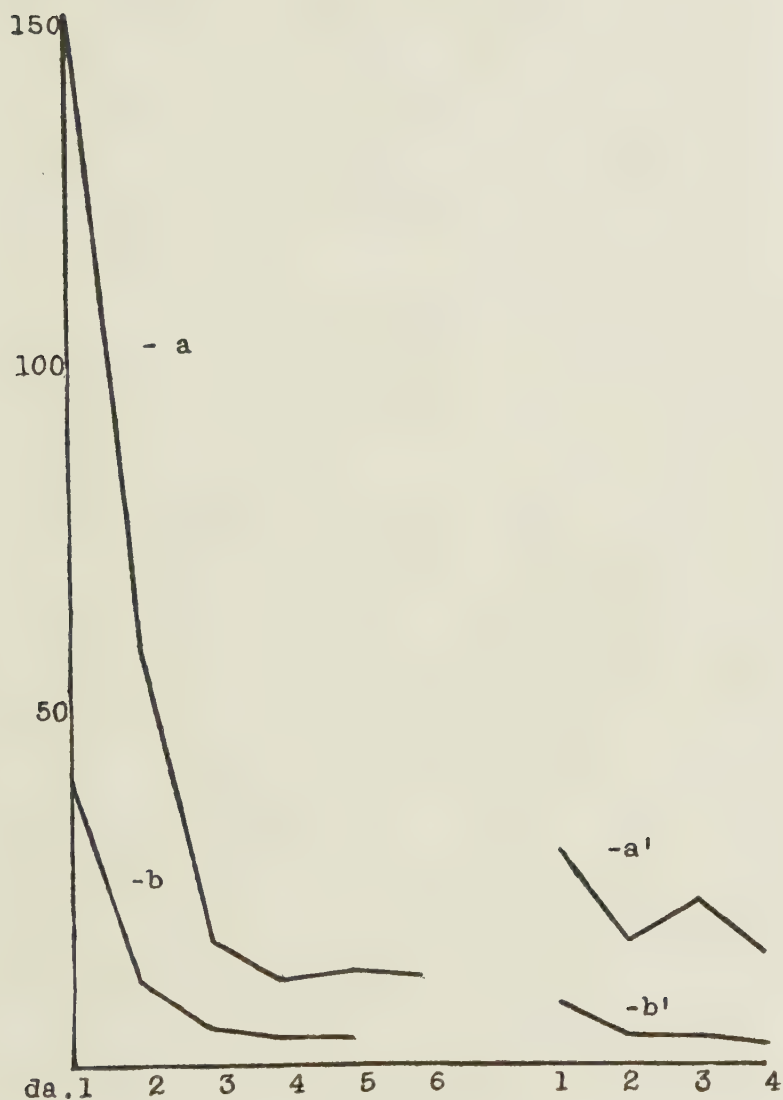


FIGURE 13

LEARNING CURVES, AVERAGE TIME IN SECONDS PER TRIAL ON CONSECUTIVE DAYS, FOR THE LATCH-BOX

a and *a'* for operated animals; *b* and *b'* for normal animals.

Rat No.	Latch at left side of door					Latch at right side				
	Days					Days				
	1	2	3	4	5	1	2	3	4	
			<i>a.</i>	<i>Normal</i>	<i>Controls</i>					
11	46	10	5	9	5	10	6	3	2	
12	18	9	8	6	4	16	6	6	4	
13	19	10	4	4	5	7	4	2		
14	21	63	28	5	5	16	9	7	3	
15	30	9	6	6		13	5	6	3	
16	17	4	1			9	3	2	1	
17	31	30	6	4		7	3	1		
18	151	8	5	1		3	3	3	1	
19	117	16	3	3	3	8	5	6	3	
20	82	12	5	3	2	5	4	1	2	
21	75	16	14	5	2	11	6	3	4	
22	78	10	4	5	3	4	12	12	5	
23	11	4	2			4	7	2		
24	44	15	7	4	3	22	2	3	3	
25	36	8	4	3		15	4	1		
26	41	7	4	5	5	6	3	3		
27	13	4	2			4	4	4	2	
28	16	14	3	3		9	3	3		
29	26	5	2	2	4	11	3	5	3	
			<i>b. Operated Cases (Double Cervical Section)</i>							
			Days							
			1	2	3	4	5	6	7	8
			<i>Latch at left side of door</i>							
1			98	28	8	3	5	3		
2			112	24	25	22	8	4	9	5
3			168	46	24	21	24	10	13	10
4			68	59	8	5	5	3		
5			309	144	19	17	29	45	21	23
			<i>Latch at right side of door</i>							
1			15	4	4	3	4	3		
2			21	8	8	4	6	5	5	
3			46	24	31	7	29	21	16	12
4			5	3	3					
5			65	47	78	63	29	33	19	37

the door while 13a' shows their rate of learning for the same mechanism on the right side of the door. Figures 13b and 13b' tell the same story for normal controls. The records upon which these curves are based are given in Table 3, which gives for each day the average time in seconds of each animal's performance. These records seem to indicate that both groups of animals show about the same relative rate of improvement in performance but that the operated animals do not reach the level of performance of normal animals. Operated cases are definitely slower in their reactions to the latch mechanism, although some operated cases are able to equal normal records.

Two cases with double section, Nos. 6 and 7 described in the protocols, were operated after they had served as normal controls on the problems. Records of their performance on the latch-box made just previous to the first operation, when compared with records made after the operations, show no impairment of ability to operate the mechanism. Records of these cases indicate no greater loss of the habit than that shown by normal animals over an equal period of time. Cases that had learned the latch mechanism after two operations evidenced no loss of the habit after periods as long as three months after original learning.

Table 4 summarizes the evidence regarding lesions, positions of lesions in the cord, maze records, the minimum time in seconds of the best performance on the latch-box, the hand preference for the latch-mechanism, and the hand used in face washing, for the cases with double cervical section of the cord. Records for

TABLE 4
SUMMARY OF DATA, CASES 1-5 INCLUSIVE, OF PROTOCOLS

No.	Tracts intact	Position of lesion (root level)		Maze records				Min. time on latch-box (sec.)	Hand used	
		L	R	Food at					Latch-box	Face wash-ing
				R T	E	T	L E			
1	pt. v.f. l. v.s-c. pt. l.d.s-c.	4	2			no record		3	R	L
2	l.v.f. r. s-c. tracts	2	5	66	16	41	18	4	?	R
3	pt. r.s-c. pt. l.v.f. l. s-c. tracts	4	2	66	41	91	21	10	L	L
4	r.v.f. r. s-c. and r. r-s. tracts	5	1	56	18	36	15	5	R	R
5	pt. l.v.f. l. s-c. and l. r-s. tracts	2	4	101	43	151	37	17	L	L

Legend: *r.*—right; *l.*—left; *v.f.*—ventral funiculus; *d.s-c.*—dorsal spino-cerebellar; *v.s-c.*—ventral spino-cerebellar; *r-s.*—rubro-spinal; *pt.*—part.

five cases are given in this table. These are the first five cases described in the protocols.

SUMMARY OF PROTOCOLS IN CASES OF DORSAL SECTION AND COMPLETE TRANSECTION

Dorsal Section in the Cervical Region. The cases of single dorsal section showed practically no permanent symptoms of injury to the cord. There was considerable motor impairment in the first days with little evidence of sensory impairment in these cases, except for proprioceptive control. At the end of a month-and-a-half period of observation they showed no signs of

defect and their general behavior and reactions to tests were quite comparable to those of normal animals.

Complete Section in the Thoracic Region. This case, No. 10 of the protocols, showed no recovery of coordinated movements other than those which can be carried out under the control of isolated spinal segments. There was no evidence for conduction past the lesion, nervous or muscular. Hooker and Nicholas (6) obtained evidence of conduction past a complete break in the cord in newborn rats which had been operated *in utero*. They found no histological evidence for regeneration of the nervous elements of the cord. They explained the conduction in terms of muscular tensions set up which might stimulate proprioceptive fibers leading to intact portions of the cord beyond the block. No evidence of such transmission of impulses either in the cephalad or caudad direction was obtained during the six months and more of observation on this animal. Histological examination showed the lesion to be complete at the seventh thoracic level.

ATTEMPTS AT CONDITIONING

Animals used for this work were a normal rat, No. 4, with double cervical section of the cord, and No. 10 with complete transection of the cord.

The animals were given break-shock stimuli applied to the left hind foot and contact stimuli, touch with the rubber end of a pencil on the thigh from which the hair had been clipped. An indifferent electrode was fastened to the back of the animal and the shock was administered to the left foot.

In the normal animal, although tests were run over a period of two months, there was never any evidence of flexion of the leg in response to touch alone. Repetition of shocks caused emotional excitement which seemed to have a facilitating effect for contact stimuli. The animal squealed in response to a rather large percentage of tactile stimuli after break shocks had been given for some time.

In the case of the completely transected animal there was no apparent effect of the stimulation at any time except for reflex jerking of the foot to the shock. This animal very frequently continued face washing while being stimulated with sufficiently strong shocks to cause violent emotional excitement in the normal animal. The case with double section of the cord responded by squealing, to the same strength of stimulation as did the normal and, after some seven hundred to eight hundred combined stimuli, he began to show a rather definite response to contact on the leg. There was pricking up of the ears and a slight turning of the head to the left side, a kind of air of expectancy, accompanied by squealing in response to about 25% of the tactile stimuli on some days.

VII

DISCUSSION

Afferent and efferent conduction past a double break in the cervical cord of the rat has been demonstrated in cases with complete section of one-half of the cord and interruption of all but the ventral and ventro-lateral funiculi of the other side. The afferent impulses so conducted include protopathic, equal conduction on both sides with complete cervical hemisection; kinaesthetic, in all cases probably impaired, but sufficient to permit walking the elevated pathway; tactile, under emotional facilitation and as evidenced by cleaning reactions for both sides of the body. Efferent impulses include initiation of scratch reflex, hind leg to head, when hemisection was complete on either the same or the opposite side; cleaning reactions, head to body, for both sides; orientation of the body in response to stimulation of the receptors of the head, in maze running; postural coordinations of rising on the hind feet in response to stimulation of the receptors of the head.

The reactions were less perfect than in normal animals, but they show that afferent impulses, tactile and protopathic, can pass a complete hemisection of the cord for the same or for the opposite side. Motor impulses can pass such blocks in the cervical cord, initiating for either side, simple reflexes, coordination between head and limbs in scratch reflexes or cleaning reactions, postural responses and orientation of the body.

THE MECHANISM OF CONDUCTION

What is the mechanism of conduction in these cases?

It may be that the intact connections of one side with the olive, the vestibular nucleus, the cerebellum, the midbrain, and the thalamus, were sufficient to carry out all functions of the limbs of both sides. This seems improbable because it is impossible to correlate either sensory or motor function with the side in which these tracts remained intact. It is improbable because of the evidence for a relationship between recovery and relative extent of lesions on the two sides. Bilateral section of other tracts, the cortico-spinal, rubro-spinal, gracilis, and cuneatus, results in no more evident bilateral disturbance than hemisection. Finally, the observations of Lashley and Ball (7) show no significant symptoms after section of the ventral and ventrolateral funiculi alone.

It may be that there are scattered long fibers in all parts of the cord which normally have all functions. This is not borne out by studies of degeneration. The few long fibers in the major tracts demonstrable by degeneration methods, which have separate origin or termination from the main part of the tract, seem inadequate to carry the mass of excitation involved in complex integrated activities.

It is possible that conduction may be by means of long fibers crossing from one-half of the cord to the other in the interval between the levels of the two sections. Degeneration studies show some such crossing for many tracts but the number of fibers is small in proportion to the bulk of the tracts. Such crossing

fibers cannot explain the phenomena observed in efferent conduction which recovers most rapidly and completely. Evidence against it is furnished by two cases in this study, Nos. 1 and 2, in which the cortico-spinal tracts were completely severed at one level. Lashley and Ball demonstrated that the cortico-spinal tract had been completely severed at one level in some of their cases and that in others the rubro-spinals had been completely severed at one level.

From the evidence now available it seems most probable that conduction in these cases of double section of the cervical cord is through arcuate systems.

CHARACTER OF RECOVERY

The question as to whether this is a normal or vicarious function remains to be answered. It is probable that conduction of all types of impulse must be a normal function of arcuate fibers. Normally it does not play the most important rôle, since reintegration is necessary after establishment of lesions. Rothmann (16) has suggested that phylogenetically old systems remain in the more highly developed species but that the higher centers have developed long and more direct paths for the control of lower centers. In the intact animal both systems function in the integration of movements. He assumes that learned movements are very largely under the control of direct paths from the higher centers, but, in the absence of such direct connections, the control may again be assumed by the more devious routes. The evidence for restitution of the control of movements in the cases studied during the

course of our experiments seems to lend support to the theory of Rothmann.

In these cases it is difficult to state how much of the reacquisition of function which occurs is due to recovery from shock, how much is due to acquisition of function vicariously by previously non-functional or other-functional tracts, and how much is to be attributed to ability to get along without the lost functions.

The picture immediately after the operation and for some time following is one of nearly complete abolition of function. Reflex responses to protopathic stimuli can be obtained a few minutes after the second operation has been completed, although in some cases, and especially in that of No. 1, there is evidence of analgesia. Gross movements of the limbs occur shortly after operation and always on the second day following but they are not well coordinated for some time. Within two to three days after operation the animals exhibit a fair degree of coordination of the limbs in locomotion. Orientation is poor at first but the animal soon learns to avoid obstacles in its path. Coordinated head-limb reflexes, face cleaning, are sometimes exhibited on the day following the operation, although they are not very effective when they first appear. This may indicate that a part of the reacquisition of function is due to recovery from shock.

The performance of the animals on the elevated pathway offers evidence of improvement in sensorimotor control with practice. No matter when they were first exposed to this situation after the operations, and the

variation in time is from six days to two hundred days after double cervical section, the animals had to have a certain amount of practice before they acquired the ability to adapt to such a situation. This holds true as well for maze and latch-box performances, in each of which there were considerable variations in the length of time after operation before the animals were started. Instances of this kind do not point to recovery from shock effects, but they indicate that the remaining connections may be improved through practice at no matter what time they may be exercised.

The animals evidently learn to get along without certain functions which are permanently lost. In all cases they survived and cared for themselves without ability to use one forelimb in finer manipulations. In the case of No. 2, although the right hand recovered sufficiently to be used in face washing, it was not used for manipulation of the latch mechanism. This animal resorted to the use of her mouth when exposed to the situation in which the lever was placed so high that it required reaching up to manipulate it with her hand. Here we have evidence of a substitutional activity which is indicative of learning to get along without a lost function.

Since there are more apparent similarities than differences in the abilities of the animals subjected to two lesions of the cord upon recovery from symptoms of such operations, it would incline one to believe that no matter what particular fibers of the ventral and ventrolateral cervical cord are intact, they may function in about the same capacity. This does not fully answer the question as to whether functions are vicariously

taken over by such cord bridges or whether there is more efficient utilization of residual functions in the portions left intact.

Observations on hemisections of the cord in monkeys led Turner (20) to conclude that "as no regeneration took place at the seat of the lesion in these experiments, the impressions were probably conveyed to the parts below the lesion by the opening up of decussating paths from the opposite uninjured side" (p. 517). After having noted the return of sensory function on both sides in cases of hemisection of the cord he stated that "it appears that in the monkey at any rate, owing probably to the less highly organized state of its spinal cord, restitution of the sensory functions occurs at a much earlier date after infliction of an injury than obtains in the highly organized cord of man" (p. 518).

Indications are that temporary shock effects play some part in the recovery of the animals but that a large part of the recovery comes about through a more efficient utilization of the remaining fiber tracts of one side of the cord which is the consequence of spontaneous use and forced exercise.

MECHANISMS OF RECOVERY

Some evidence has been obtained in this study as to the mechanisms concerned in recovery. No. 10, with complete transection of the cord at the level of the seventh thoracic root, has demonstrated the limited capacity of recovery in isolated segments of the cord. There was no recovery of movements except those of a purely local reflex nature and, at no time, any evidence

of conduction past the complete break in the cord. There was never any sign of coordination of movements of the hind limbs with those of the forelimbs in this animal.

It is possible that the necessity of conduction past the break is a factor in recovery. Necessity for practice of a limb may have an influence in its recovery. The work of Oden and Franz (11) has shown that little recovery took place in paralyzed members unless they were subjected to special treatment and forced into use. No. 3, of our double cervical cases, with the minimal lesion on the left side, used the left forepaw for finer movements and showed no recovery of the right forepaw for such activities. The lesion on the right side in No. 3 was no greater than the lesion on the left side in No. 1 who recovered the use of her left forepaw for face washing. That this recovery took place in No. 1 may be due to the fact that all long tracts on the right side of the cord had been completely severed in this animal. Exercise achieved as a consequence of stimuli applied to the body and head may have been a factor in more ready adaptation on the part of other animals as well. Definite efforts were made to excite head reactions to the body as well as to stimulate limb reactions to the head. The fact that any reaction was obtained in the first place, however, indicates that paths for the passage of such impulses must have been open from the beginning.

There are indications that recovery may be related to the length of the intervening segment of the cord between the two lesions. Nos. 3 and 5, each with lesions

in the second and fourth cervical root levels, remained slow in movements generally and showed the poorest records of all in the maze and latch-box. The failure of No. 5 to adapt to the simple maze is the more surprising in view of the fact that she was able to relearn an 8-cul-de-sac maze without much evidence of loss, after her failure on the simple maze. It was most difficult to keep these two animals in good physical condition, no matter how well they were cared for. On the other hand, No. 4, with lesions exactly similar to those of No. 5 except that they were more widely separated, gave evidence of much better control of movements generally and made much better maze and latch-box records. No. 2, with lesions in the second and fifth cervical root regions, also affords evidence that separation may be a factor in recovery. Her performance on the maze and latch-box closely approaches that of No. 4 even though her lesions were more severe. The only contradictory evidence furnished is that of No. 1 whose lesions were more severe and no farther separated than those of Nos. 3 and 5. Her performance on the latch-box, so far as time records are reliable, was closely similar to that of Nos. 2 and 4. Unfortunately, maze records were not obtained for this animal.

Some bits of evidence seem to point to a relation between defects and completeness of section. No. 1, with very severe section, seemed to give the clearest evidence of protopathic disturbance, but this observation was for only a short period after the lesions were established. Two cases, Nos. 4 and 5, in which the rubro-spinal

tracts of one side were intact, seemed to have the least difficulty in adjustment to the elevated pathway. Considering the two lesions in the same animal, it was evident that recovery of finer manipulations of the forearm occurred on the side of the least complete lesion.

That emotional reinforcement may be a factor in passage of the block by impulses has been indicated by observations on several cases of double cervical section. As previously noted, responses to tactile stimulation are difficult to interpret in the rat. It was found fairly easy to elicit squealing to contact stimuli on the parts of the body caudad to the lesions when the animal had previously been subjected to moderately strong faradic stimulation on the body and limbs. This reinforcement was evident for some little time after a series of faradic stimuli had been given. The fact that emotional reinforcement seems to operate under such a condition may have some relation to recovery by a process of irradiation or spreading of the effects of localized stimuli.

MODIFIABILITY IN SEPARATE SPINAL SEGMENTS

The work done on conditioning in this study has afforded no evidence for conditioning or modifiability of isolated spinal segments. There is some evidence of conditioning or facilitation in cases where a limited connection remains with the head region. Further investigation of this question is necessary before any conclusion can be drawn about the possibility of establishing conditioned reflexes in animals with double cervical section of the cord.

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LES MÉCANISMES COORDONNANTS DE LA MOELLE ÉPINIÈRE

(Résumé)

On a fait cette étude dans le but d'obtenir de l'évidence relative aux problèmes de la conduction spinale et de la récupération des effets des lésions dans la moelle épinière. On s'est servi des rats adultes albinos et pigmentés. On a fait subir des lésions de la moelle aux animaux. On a préparé quelques cas avec une hémisection double de la moelle cervicale; d'autres avec une section de la colonne dorsale et des fibres radicales dorsales seulement; un cas avec une section complète de la moelle au septième niveau thoracique.

On a fait des observations de la récupération sensorielle et motrice. On a fait des tests de sensibilité à divers temps après les opérations. On a fait des observations du rat s'estant récupéré du contrôle moteur dans la station debout, la marche, la course, l'action de grimper, et l'action de creuser. On a fait des tests des coordinations de la tête et des membres. On a testé l'apprentissage moteur au moyen d'un parcours élevé, d'un labyrinthe simple en forme de T, et de la "latch-box." On a essayé d'établir des réflexes conditionnels.

Des tableaux dans le texte montrent l'étendue des lésions dans les animaux individuels employés dans cette étude.

La conduction afférente et efférente au-delà d'une cassure double dans la moelle cervicale du rat s'est montrée dans des cas avec une section complète de la moitié de la moelle et l'interruption de tous les funiculaires sauf les ventraux et les ventro-latéraux de l'autre côte. Les impulsions afférentes ainsi conduites comprennent une conduction protopathique égale des deux côtés avec une hémisection cervicale complète; kinésique, dans tous les cas probablement affaiblie, mais suffisante pour permettre aux animaux de marcher sur le parcours élevé; tactile, sous la facilitation émotionnelle et montrée par des réactions de nettoyer pour les deux côtés du corps. Les impulsions efférentes comprennent; l'initiation du réflexe de gratter, la jambe de derrière à la tête, avec une hémisection complète du même côté ou du côté contraire; des réactions de nettoyer, la tête au corps, des deux côtés; l'orientation du corps en réponse à la stimulation des récepteurs de la tête, dans le parcours du labyrinthe; des coordinations posturales de se lever sur les pattes de derrière en réponse à la stimulation des récepteurs de la tête.

Les segments isolés de la moelle montrent la récupération des réflexes locaux seulement avec nulle évidence de la conduction au-delà de la cassure dans la moelle. Il n'y a nulle évidence de conditionnement dans la moelle isolée et très peu d'évidence dans les conditions de l'expérience, dans le cas avec une section double de la moelle ou dans l'animal normal. Les animaux avec une section de la portion dorsale de la moelle cervicale montrent très peu d'évidence de symptômes permanents.

On a fait des suggestions à l'égard des mécanismes de conduction et de la récupération dans les cas de la section double de la moelle cervicale.

INGEBRITSEN

DIE KOORDINATIONSMEKANISMEN DES RÜCKENMARKS

(Referat)

Es war der Plan dieser Untersuchung, die Aufgaben der Rückenmarksleitung [spinal conduction] und der Genesung von den Einwirkungen von Verletzungen des Rückenmarks experimentell zu behellen. Es wurden erwachsene Albinoratten und behaubte Ratten verwendet. Es wurden an den Tieren Verletzungen des Rückenmarks ausgeführt. Einige Fälle wurden mit doppeltem Halbschnitt des Nackenmarks präpariert, einige mit Schnitt bloss der Dorsalsäule und der Stränge der Dorsalwurzel; in einem einzelnen Fall wurde das Rückenmark am Niveau des siebenten Brustnerves vollkommen durchschnitten.

Es wurden Beobachtungen gemacht an der sensorischen und motorischen Wiederherstellung. Es wurden, zu verschiedenen Zeiten nach den Operationen, Prüfungen der Empfindung [sensitivity] gemacht. Es wurden Beobachtungen gemacht an der Wiederherstellung der motorischen Beherrschung des Stehens, des Gehens, des Laufens, des Kletterns, und des Grabens. Es wurden Prüfungen der Zusammenwirkung [coordination] zwischen Kopf und Glied gemacht. Man prüfte die motorische Lernfähigkeit mit einem erhöhten Geleise [elevated runway], mit einem einfachen T-Labyrinth [T-maze], und mit dem Klinkkasten [latch-box]. Man versuchte, bedingte Reflexe zu bilden.

Figuren in Text weisen auf den Umfang der Schädigungen bei den einzelnen, in dieser Untersuchung verwendeten, Tiere hin.

Die afferente und efferente Leitung über einen doppelten Bruch des Rückenmarks der Ratte ist in Fällen demonstriert worden, in denen die eine Hälfte des Rückenmarks vollständig getrennt worden war und in denen auf der anderen Seite alle Funiculi mit Ausnahme der ventralen und ventrolateralen in ihrer Leitung unterbrochen worden waren. Die auf diese Weise weitergeleiteten afferenten Impulse sind u.a.: (1) Protopathische: Gleiche Leitung auf beiden Seiten bei vollständiger Hemisektion des Nackenmarks; (2) Kinesthetische: In allen Fällen wahrscheinlich beeinträchtigt, aber genügend zur Ermöglichung des Gehens auf dem erhöhten Geleise; (3) Tastimpulse: zeigen sich unter Einwirkung der affektiven Bahnung [facilitation] und werden an Reinigungsreaktionen auf beiden Seiten des Körpers erwiesen. Die erwiesenen efferenten Impulse schliessen in sich ein: Einleitung des Kratzreflexes (Hinterfuss an den Kopf), bei vollständiger Hemisektion entweder der selben oder der entgegengesetzten Seite; Reinigungsreaktionen (Kopf an den Körper) auf beiden Seiten; Orientierung des Körpers als Erwiderung auf Reizung der Rezeptoren des Kopfes beim Labyrinthlaufen; Haltungs koordinierungen [postural coordinations] des Sich-Erhebens auf den Hinterbeinen als Reaktion auf Reizung der Rezeptoren des Kopfes.

Isolierte Segmente des Rückenmarks erweisen Wiederherstellung der lokalen Reflexe allein, ohne Beweis der Leitung über den Bruch im Rückenmark. Man erhielt keinen Beweis der Bedingung im isolierten Rückenmark und wenig Beweis für die Bedingung sowohl bei doppelter Sektion des Rückenmarks wie beim normalen Tiere, unter den Bedingungen dieser Untersuchung. Tiere mit Sektion des dorsalen Teils des Nackenmarks geben wenig Beweis dauernder Symptome.

Es sind Anweisungen gegeben worden in Bezug auf die Mechanismen der Leitung und der Genesung in der Fällen doppelter Sektion des Nackenmarks.

INGEBRITSSEN

